



The role of mycorrhizas in plant community structure and dynamics: lessons from grasslands

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Introduction

Research on the mycorrhizal associations over the past several decades has yielded increased understanding and appreciation of the important role of this symbiosis in the functioning and performance of plants in a wide array of terrestrial ecosystems. We now understand that the role of mycorrhizal fungi extends beyond the symbiotic acquisition of phosphorus for the host plant and reciprocal carbon provision from the host to fungus. Additional effects of mycorrhizal fungi on the functioning of their host plants including increased disease resistance, improved water relations, acquisition of other soil nutrients, and alterations in other soil physico-chemical properties have been documented. Other aspects of the ecology of mycorrhizas, including variation in the costs and benefits of carbon and nutrient exchange, the ecological significance of mycelial networks, the role of mycorrhizal symbiosis in multi-species interactions, and the extent and consequences of host-specificity in these associations have also recently been explored.

The effects of mycorrhizal fungi on the function and growth of individual plants have numerous consequences that extend to the plant population and community levels. The costs and benefits of colonization by mycorrhizal fungi for plant resource availability can strongly influence patterns of plant reproduction and demography, responses to competitors, herbivores, and other biotic interactions, and patterns of species composition, diversity, and succession. This ancient mutualistic symbiosis may be one of the most important but least understood biotic interactions regulating plant community structure and dynamics. Hopefully, an increased understanding of these patterns, their underlying mechanisms, and the costs and benefits of this symbiosis will lead in the future to the formulation of general predictive theory of mycorrhizal effects on plant communities.

In this paper, we examine the consequences of mycorrhizal symbiosis at the plant community level, with a primary focus on grasslands. Mycorrhizal fungi are ubiquitous and abundant in grasslands and savannas worldwide (e.g., Chiariello et al., 1982; Davidson and Christensen, 1977; Fitter, 1986; Koide et al., 1988; Miller, 1987; Newsham and Watkinson, 1998; O'Connor et al., 2001; Perez and Frangi, 2000; Smilauer and Smilaveraer, 2000; van Auken and Brown, 1998). Indeed, our sampling of >100 herbaceous species in North American tallgrass prairie and southern African low veld grasslands revealed that all species thus far examined are colonized by mycorrhizal fungi and that most dominant grasses in these systems are obligate mycotrophs. In addition, studies over the past decade have demonstrated that mycorrhizas have particularly large influences on several aspects of grassland community and ecosystem functioning, and experiments in grasslands have contributed much to the lessons learned and new questions raised about the ecological role of this symbiosis. Here we review evidence for the varied effects of mycorrhizas on the composition and diversity of plant communities, discuss the various hypothesized mechanisms by which mycorrhizal fungi influence plant community structure, and explore the role of this symbiosis in the broader context of the complex array of biotic interactions characteristic of grasslands and many other terrestrial ecosystems.

Mycorrhizas and plant community structure

The processes regulating the composition and diversity natural communities has been a central focus in ecology. The roles of species interactions, natural disturbances operating at different scales, and historical and biogeographic factors have all been explored (e.g., Brown, 1995; Huston, 1994; Pickett and White, 1985; Ricklefs and Schluter, 1993). Studies of the

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role of biotic interactions influencing plant community structure have focused largely on plant competition and plant-herbivore interactions (e.g., Frank et al., 1998; Grace and Tilman, 1990). The important role of mycorrhizal symbiosis in shaping plant community structure has recently become recognized and gained significant attention. This has been a result of both a general increase in research on mycorrhizas, and an increasing recognition that positive interactions (e.g., direct and indirect facilitation) are common in natural communities and may have large effects on plant community structure (Bengtsson et al., 1994; Callaway, 1995; Clay and Holah, 1999).

Recent studies have shown that mycorrhizal fungi can have large but quite variable effects on plant species diversity, composition, and successional dynamics (e.g., Allen and Allen 1984; Connell and Lowman, 1989; Grime et al., 1987; Hartnett and Wilson, 1999). There is also increasing evidence that the effects of mycorrhizal fungi on their host plant communities are context-dependent, varying with host species, plant life history stage, resource availability, and abiotic conditions (e.g., Bethlenfalvay et al., 1982; Fitter, 1986; Francis and Read, 1995; Hartnett et al., 1994; Johnson et al., 1997). In some herbaceous communities, mycorrhizas enhance plant species diversity by increasing the establishment and abundance of subordinate species relative to the community dominants (Gange et al., 1993; Grime et al., 1987; Newman and Reddell, 1988), and plant diversity may be positively correlated with the species diversity of mycorrhizal fungi (van der Heijden et al., 1998a). In other communities, evidence indicates that mycorrhizal fungi decrease plant species coexistence and diversity (e.g., Hartnett and Wilson, 1999; Newsham et al., 1995; O'Connor et al., 2001). Experiments in both North American tallgrass prairie (Figure 1) and European calcareous grasslands (Zobel and Moora, 1995) indicate that mycorrhizal symbiosis decreases plant species diversity by increasing the competitive success and abundance of the community dominants relative to subordinate species. Studies in other grasslands and grassland restorations indicate that mycorrhizal fungi may also alter species composition with no net effect on species richness (Smilauer and Smilauerova, 2000), or may alter rates of succession by hastening the displacement of ruderal species by native grasses (Smith et al., 1998).

Thus, it is clear that at the local community (alpha) scale, mycorrhizal fungi have the potential either to decrease or increase plant species diversity, al-

ter plant species composition, and/or influence the rate and trajectories of community succession. The hypothesized underlying mechanisms causing these observed effects of mycorrhizas on plant communities are similarly varied and include: (1) direct and differential effects on plant species traits such as colonization, establishment, and competitive ability, (2) effects of mycorrhizal mycelial networks and inter-plant resource transfer through hyphal connections on plant growth and relative abundances, and (3) mycorrhizal mediation of other biotic interactions such as plant-herbivore or plant-pathogen interactions. In the following sections, we review the evidence and discuss various proposed mechanisms for mycorrhizal influence on plant communities.

Patterns of plant species diversity in nature are scale-dependent, and conservation of biodiversity at the regional or global scale should not be confused with maximization of species richness and diversity at the local community or patch scale (Poiani et al., 2000). Many natural grassland communities are and have historically been characterized by low diversity and high dominance at the local community (alpha) scale. In these systems, this low local patch diversity, coupled with significant heterogeneity at larger scales, results in a pattern of higher diversity at the landscape or regional scales. Furthermore, high alpha diversity at the local community scale is often associated with a larger number of invasive exotic or ruderal species, whereas stable, undisturbed communities are characterized by lower richness. Thus, high alpha diversity or species richness at the local scale is not necessarily a good indicator of the biotic integrity or stability of a community. The study of mycorrhizas or any other factors that influence patterns of diversity must consider spatial scale, and focusing solely on the maximization of local species richness as a conservation goal is an unwarranted oversimplification and generalization that ignores scale and overemphasizes species numbers relative to species composition and relative abundances. It is clear from the various studies reviewed above that mycorrhizas have large influences on plant community structure and are an important factor in the stability of plant species composition, as evidenced by the large magnitude of changes in plant communities reported in response to experimental alteration of mycorrhizal activity.